SOME CHARACTERS OF XYLEM TISSUE IN CYCADS

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(WITH PLATES XXXVII, XXXVIII AND ONE FIGURE)

The detailed investigation of certain anatomical features of the Cycads has been undertaken in the hope of throwing light on the origin of the more specialized structures occurring in the higher Gymnosperms. In recent years considerable work has been devoted to determining the details of anatomical structure in the Conifers. These details have been given much prominence as evidences of the inter-relationships of the various groups. A lack of knowledge of the ancestry of the structures themselves, however, has minimized their value as criteria in phylogenetic investigations. This knowledge can be supplied only by a study of primitive forms.

Pitting

The shape and arrangement of bordered pits in the woody tissue have long been regarded as valuable phylogenetic data. It is largely owing to these features that the Araucarians have been supposed to be closely related to Cordaitean forms, and many botanists still hold this view, notwithstanding the arguments advanced by JEFFREY (6) and SEWARD (9) in favor of different lines of ancestry for the family. In 1907 GOTHAN (4) worked out a phylogenetic line of development of bordered pitting, considering the most primitive type to be hexagonal and crowded over the whole tracheid wall. According to his theory, the pitting next became eliminated from the tangential walls, but still covered the radial as before. A further elimination resulted first in small isolated groups of pits, then in the uniseriate flattened condition, and finally in the scattered arrangement, where the pits occur singly on the tracheid wall. This series of eliminations took place on the middle part of the wall of the tracheid, the crowded arrangement being retained on the ends to facilitate vertical movement of the sap. GOTHAN found his types of arrangement combined in a fossil plant, but in no living form.

JEFFREY is more conservative than many others in his estimate of the significance of pitting, but considers that it is of distinct value in classification when its character in all parts of the plant is considered. On this ground, in his work on the Araucarineae, he accepts the presence of opposition pitting in the cone axis, and scattered pits in the seedlings, as denoting descent from an Abietineous type. He has neglected the character of the pitting in primitive forms such as the Cycads, however, and his interpretation is not in harmony with the facts which these forms disclose. This was done, notwithstanding the fact that as early as 1840 DON (2) recognized the value in phylogeny of the study of Cycads. He carefully worked over the character of tracheids by such methods as were in vogue at that time, and agreed with MEYENS, a still earlier investigator, that the spiral, scalariform, reticulate, and border-pitted types could be referred to a common origin. The importance of these transitions was emphasized also by PENHALLOW (7) in 1907 as affording valuable data on the ancestral character of the bordered pit of the higher forms. In 1919 BAILEY (1) argued that opposite pitting is formed by the breaking up of bordered scalariforms, and that the alternate type was formed from this by a "staggering" of the rows of pits.

In this paper certain features of the primary wood of the Cycads will be considered first. Fig. 1 is a longitudinal section of the petiole of *Cycas revoluta*, showing the tangential walls of the tracheids in the neighborhood of the protoxylem. The tracheid *a* shows the characteristic spiral and scalariform structure of the protoxylem. In transverse section (not figured) the scalariform bars are seen to arch over the intervening spaces so as to form very narrow borders. On the cell *b* the scalariforms are more closely approximated, and through the slits may be seen shorter pores, belonging to the adjacent wall of the next tracheid. The tracheid *c* also shows this clearly. In the other two tracheids typical bordered pits are present. The type of scalariform from which such bordered pits are formed is shown in fig. 2. It is a scalariform similar to that formerly described, except that the borders are wider. Fig. 3, another section from a *Cycas* petiole, indicates transitions in the formation of ordinary bordered pits from this

type of scalariform. Below the center of the figure is a scalariform reaching from side to side. Its border shows constrictions at two points, evidently the beginning of a division into three bordered pits. In the portions of the tracheid above and below, complete divisions and other incomplete ones are in evidence. The name "fusion pits," which has been applied to similar appearances, is evidently a misnomer in this case. They plainly represent phases in the breaking up of the ancestral scalariform rather than the union of two of the more specialized bordered pits. The small pits on tracheids *a* and *b* of fig. 1 in all probability are formed from the narrow bordered scalariforms in a similar manner.

Figure 4 is a much lower magnification of a longitudinal radial section of the fossil stem of *Lyginodendron Oldhamium*, acknowledged to be one of the most ancient of the seed plants. This form had attained in the secondary wood of its stem the condition represented in GOTHAN'S second type, the pits being practically eliminated from the tangential walls (cf. SCOTT 8), but crowding the radial walls from end to end of the tracheid. Wherever the cell wall is present in the figure it is seen to be completely covered with the type of pitting known as recticulate. A careful examination of the pits shows them to be of the same type as those in fig. 1, which had their origin in the narrow bordered scalariforms.

The stem of *Cordaites* (fig. 5) has pits which, like those of the Cycads, have probably originated from the cutting up of wide bordered scalariforms, a condition quite in keeping with the general higher type of wood structure exhibited in the Cordaitean forms.

Further evidence of the origin of the bordered pit from the scalariform is found in the secondary wood of certain of the Cycads. A type of fusion pit which recalls the condition in the narrow bordered scalariforms of fig. 1 is shown in fig. 10, which is a radial section of the stem of *Dioon spinulosum*. The three pits nearest the top are of the short, slightly flattened type quite common in these forms. The next three are more elongated. All show the characteristic cross pores of adjacent elements. The seventh of the series is a pit of the second fusion type. It appears like two pits, each with a short pore, with a common long pore crossing both.

On one tracheid wall (in this case the one beneath) two separate pits have formed, each with its own pore; while on the adjacent wall of the next tracheid, one large, somewhat scalariform pit has been retained. Just below this comes a pair of completely separate pits, from their shape and approximation evidently formed by the division of what potentially was a single long one. Then come two more pits of the fusion type, after which the regular type of pitting is resumed. Such examples are often found at the ends of tracheids, where, as noted later, there are other primitive characters.

The multiseriate condition is the most common arrangement of pits in Cycads. In some cases the pits are so closely approximate as to appear slightly flattened. This is the typical condition in the Cordaiteae as described by SCOTT, and has generally been considered the most primitive bordered condition, although more specialized than the reticulate type. The outline of the pits in the Cycads, however, is more often curved.

In the Cycads the scattered type of pitting is also found, originating by the elimination of pits from portions of the tracheid. Fig. 6 from a radial section of a *Dioon spinulosum* stem shows this feature. In the lower part of the right hand tracheid we have biseriate pitting covering the radial wall, with here and there a pit obliterated. The position of the vanished pits is indicated by lighter areas caused by the thinning of the primary wall. These are the primordial pits of Sanio, which have formed as if bordered pits were to be located over them as usual. Farther toward the top is a single row of somewhat flattened pits, an arrangement common in the Araucarians. Still farther up some of the pits have become smaller, while others have been eliminated entirely, thinning of the primary wall being visible here and there. This scattered pitting is seen also in other tracheids of the figure, the primary pit areas being very evident, especially just above and below the center of the second tracheid from the left. At the center is an interesting small bordered pit surrounded by a slightly larger area, probably the boundary of the primordial pit. This seems like a case of partial elimination. The irregular obliteration of the pits has left in some places isolated groups of pits like those

referred to by GOTHAN. A further eccentricity of the elimination is illustrated in the tracheid to the right of fig. 11. The lighter colored pits have typical bilateral borders, while the obscure ones are unilateral, the corresponding pit on the overlying tracheid not having been formed.

The arrangement of pits, opposite or alternate, deserves notice. In fig. 6 two or three pits occur in a horizontal row. In some cases as many as four such pits have been found. In the more common condition, not figured, the pits are regularly alternate, sometimes round, and sometimes flattened by mutual contact. Just as the scalariforms of one tracheid are horizontal while those of the next are inclined, and either straight or curved and irregular (fig. 1), so on one tracheid is found the opposite arrangement of pits, and adjacent to it the alternate. There seems no reason for believing that alternate pitting is formed by any disarrangement of rows of round bordered pits. More specialized plants have one or other of these types predominating; for example, the alternate and flattened arrangement in Araucarineae, and the scattered, grouped, and opposite in the Abietineae. The presence of all these conditions in mature Cycad wood, as well as in the ancient fossil form described by GOTHAN, modifies to a great extent their phylogenetic significance in higher forms. It strengthens BAILEY'S statement that the presence of opposite pitting as well as alternate in the cone axes of Araucarians cannot properly be used as an argument for their descent from the Abietineae, and neither is the same condition in primitive parts of pines an evidence of descent from an Araucarian type. It would seem that if these facts have any significance in phylogeny, they indicate that both pines and Araucarians are descended from lower forms which contained both these arrangements.

It may be stated in passing that both opposite and alternate arrangements of pitting occur in the Cordaiteae, the alternate, however, being greatly predominant. Instances of opposition pitting in Cordaites may be seen in fig. 5, in the upper part of the right hand pitted tracheid. There is an example also near the lower end of the second tracheid to the left of it. Instances of GOTHAN'S grouped arrangement are also present, especially in the

lower central part of the figure. The uniseriate and scattered arrangements occur, being formed probably by the suppression of pits, as in the Cycads. The only evidence of this in the fossil section, however, is the decreased size of many of the pits in the region of elimination. A careful examination of fig. 5 will make this point clear.

It will be seen from the foregoing account that the Cycads, besides giving indication of the mode of formation of the bordered pits from the scalariform type, afford valuable data on the interpretation of the arrangement of pits. The elimination in these low

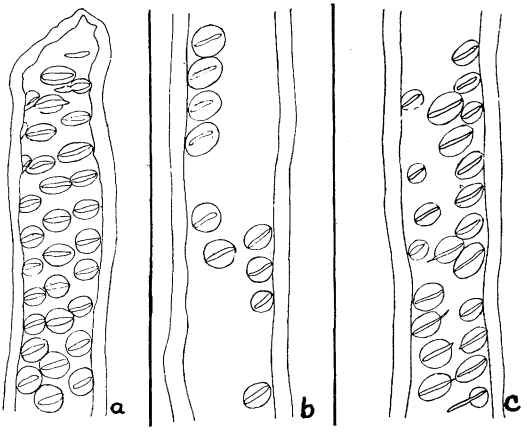

FIG. 1.—*Cycas revoluta:* radial views of different regions of tracheid from stem; *a*, end of tracheid; *b*, normal pitting at contact of two tracheids; *c*, pitting in contact with medullary ray.

forms shows no indication of following a definite law, but proceeds promiscuously, giving rise to all the various types of pitting. It is practically restricted, however, to the middle part of the tracheid, the terminal portions and those parts in contact with the ray cells remaining multiseriate.

The terminal and ray pitting of the tracheids has always remained primitive in another respect. This is indicated in text-fig. 1, which is from a tracheid of the stem of *Cycas revoluta*. In this figure *a* represents the terminal pitting, *b* the ordinary pitting, and *c* the ray pitting of the same tracheid. The pits and their pores are longer in *a* and *c* than in *b*. The pores often extend

beyond the borders in *a* and *c*, and thus recall the condition where pits are forming on scalariform elements (fig. 3). Many of the pores were measured for definite comparison, and the tracheid figured does not exaggerate the difference in pit and pore lengths. Ray pitting on *Dioon spinulosum* secondary stem wood is shown in fig. 9. Here also the multiseriate pitting is present, accompanied by the elongated pore. The left hand tracheid of fig. 11 shows the same type of pore, where a vertical parenchyma cell is in contact with a tracheid. Evidently the primitive type of pore occurs wherever a tracheid is in contact with any type of parenchyma cell. Similar primitive features have been recorded by THOMSON (11) in Araucarian ray pitting.

Tertiary thickenings are common on the tracheid walls, taking the form of spirals or scalariform bars with long shallow pits between. They occur whether bordered pits are present or not, and often traverse the region of the border itself, but have never been observed to cross the pores. PENHALLOW regarded such thickenings as relics of the ancestral manner of deposition of the cell wall, a view which is strengthened by their presence in these low forms.

Bars or rims of Sanio

Considerable importance was attached for some years to the presence or absence of "bars" or "rims" of Sanio. Miss GERRY (3) in 1910 showed them to be present in all families of the Conifers except the Araucarians, and made this a distinguishing feature between both fossil and living Araucarians and other coniferous forms. JEFFREY (6) and THOMSON (11), however, in practically simultaneous publications described bars from the transitional region of the pitting in the cone axis of an Araucarian. This JEFFREY interpreted as evidence of the derivation of Araucarians from the Abietineae. He recognized that this evidence would be invalid if all primitive types of pitting had bars of Sanio, and looked for them in primitive regions of *Cycas* but failed to find them. Their presence here was described later by the writer (10), and invalidates his conclusions. JEFFREY'S misstatement has no doubt been responsible for the exaggeration of the importance of

the structure, and probably led to the rejection of all other criteria, making the bar "an infallible test for tribal affinities" (HOLDEN 5), both in fossil and living Conifers.

In 1919 BAILEY (1) studied the origin and development of bars of Sanio, and concluded that those in transition regions are merely normal middle lamellae left between thinned pit areas in the primary wall. He states that when the pits are opposite the bars go smoothly from side to side of the tracheid, because the pits are formed on one primary scalariform pit area, and the bar is the thickening of the lamellae between this area and the next. This theory, however, will not explain the bars figured in the writer's paper of 1915. Those shown in *Araucaria* are connected with pits in regular horizontal rows, but still fork, following round the circumference of each pit, so as to leave clear diamond-shaped areas bounded by opposing forks. These small areas cannot be considered to be other primary pits. The same fact holds for the bars in the *Cycas* petiole, which fork, and are even split into two separate rims in some cases, although the pits are not far enough apart to make it possible to attribute the thin space to another primary pit area.

Bars of Sanio have now been found in other portions of Cycads than the transitional primary xylem. Figs. 6 and 7 illustrate them in the stem wood of *Dioon spinulosum*. These bars often extend beyond the margins of the pits with which they are in contact, as in the middle tracheid of fig. 7 near the bottom, and so are of a higher type than those figured in the former paper. They are still much more primitive than those of the Abietineae, however, lying in close contact with the pits, whenever such are present. Fig. 6 shows the ordinary type of bar in this plant. Between the pits of the single row on the right are bars of the regular Araucarian type. Their length is not greater than the borders to which they cling, and they spread slightly at the ends. The pitting of this tracheid is conspicuously of the opposite type, so that if BAILEY'S theory of the origin of the bars is entirely correct, they should in this case pass beyond the pits to the limit of the tracheids. In the two left-hand tracheids of fig. 6 is shown a condition which is quite common, namely, the presence of these bars in connection

with primordial pits from which the secondary pitting has been eliminated.

Trabeculae

These spool-shaped bars, extending in radial series across the lumens of adjacent tracheids, have received considerable notice in literature, owing to the confusion which arose in some cases between them and bars of Sanio. They have not before been figured in the Cycads, but are present, as shown in fig. 8, a radial section of *Dioon spinulosum* stem. They contain a core or axis composed of a substance which stains in the same way as the middle lamella of the cell. This core pierces the tangential secondary walls of the tracheid and joins up with the middle lamella. These structures are present in higher forms, but their significance is not known. Since they connect with the primary wall, they must have been laid down before the beginning of secondary thickening.

Summary

1. A study of the primary and secondary wood of Cycads indicates the development of reticulate, alternate, and opposite pitting directly from scalariform types.

2. The grouped, uniseriate, and scattered pitting characteristic of higher forms is shown to be formed by the elimination of pits. In low forms, of which the Cycads are a type, this elimination proceeded without apparent order, forming all types of grouping indiscriminately.

3. Similar arrangements of pits occur in Cordaites, although its type has become more fixed than is the case in the Cycads.

4. The Cycads, like the Araucarians, have more primitive types of pitting at the ends of tracheids and where they come in contact with parenchyma.

5. The xylem of certain of the Cycads quite commonly exhibits spiral tertiary thickenings.

6. Bars of Sanio of the Araucarian type are found in both primary and secondary Cycad wood. An elongated type of bar is also present. The Araucarian type is considered the most primitive in living seed plants. No explanation of its origin is offered by BAILEY'S theory.

7. Trabeculae are present.

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DESCRIPTION OF PLATES XXXVII, XXXVIII

PLATE XXXVII

FIG. 1.—*Cycas revoluta:* petiole; tangential section of primary wood; ×225.

FIG. 2.—*Zamia integrifolia:* petiole; pitting of primary wood; ×445.

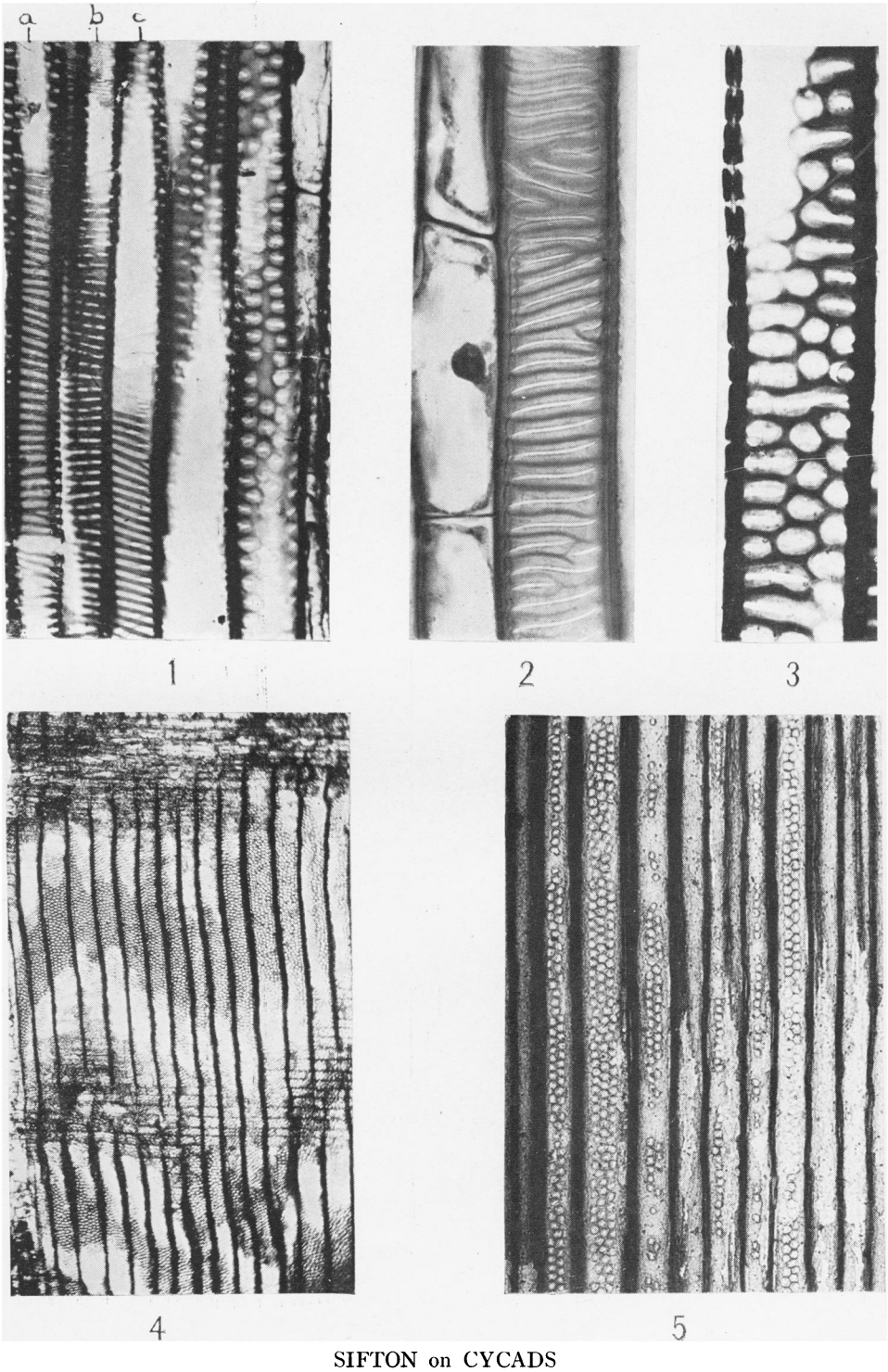
FIG. 3.—*Cycas revoluta:* petiole; primary wood, showing transitional pitting; ×445.

FIG. 4.—*Lygenodendron Oldhamium:* radial section of secondary wood of stem; ×100.

FIG. 5.—*Cordaites* sp.: radial section of secondary wood of stem; ×225.

PLATE XXXVIII

FIG. 6.—*Dioon spinulosum:* radial section of secondary wood of stem, showing pit arrangement and bars of Sanio; ×225.



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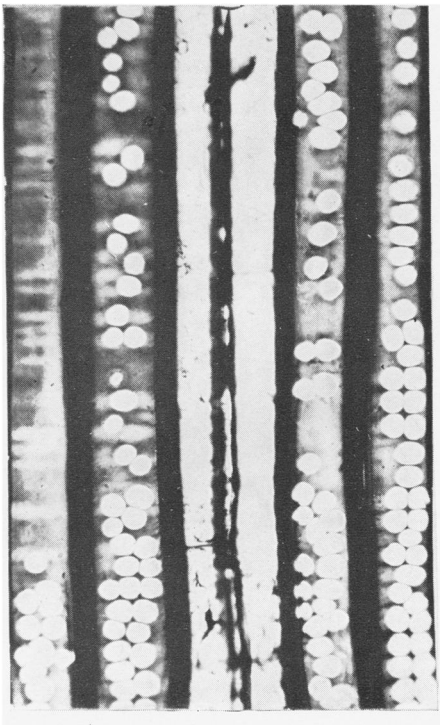

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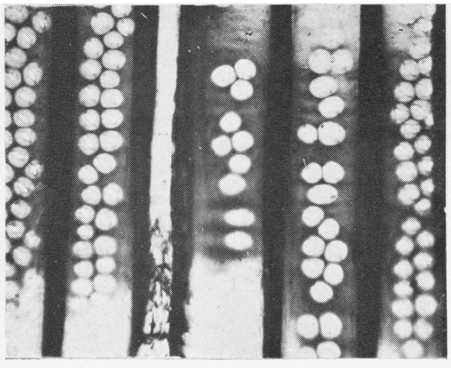

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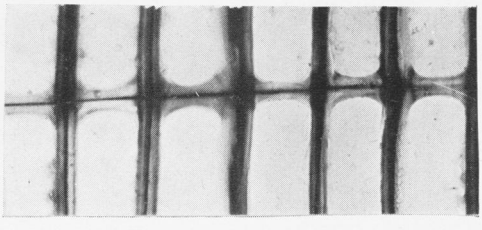

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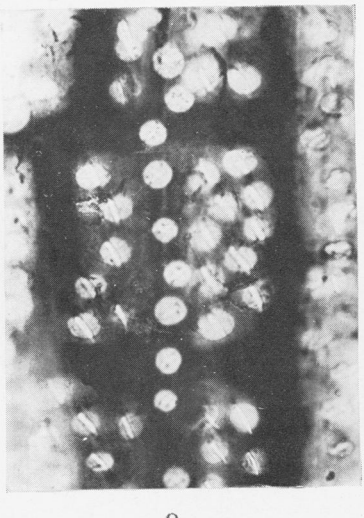

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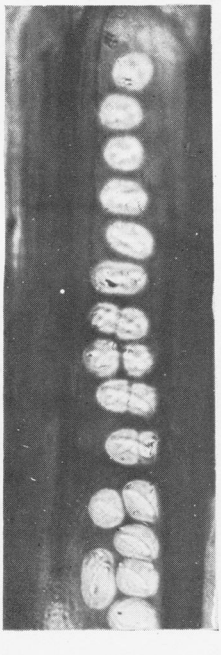

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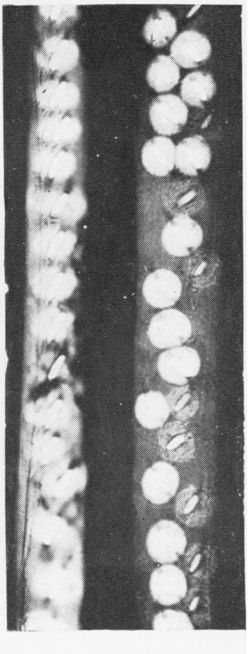

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FIG. 7.—*Dioon spinulosum:* radial section of secondary wood of stem, showing pit arrangement and bars of Sanio; ×225.

FIG. 8.—*Dioon spinulosum:* radial section of secondary wood of stem, showing trabeculae; ×225.

FIG. 9.—*Dioon spinulosum:* radial section of secondary wood of stem, showing pitting in contact with medullary ray; ×445.

FIG. 10.—*Dioon spinulosum:* radial section of secondary wood of stem, with fusion pits near end of tracheid; ×445.

FIG. 11.—*Dioon spinulosum:* radial section of secondary wood of stem, showing pitting in contact with wood parenchyma, and unilateral pits between two tracheids; ×445.